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THE ORIGIN OF THE MAMMALIA.[1]

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THE most important problems in vertebrate morphology at the present time are the connections which once existed between the great vertebrate classes. As regards the three lower classes, the present state of opinion is as follows: The Amphibia are derived by Pollard, Cope, Dollo, and Baur from the ancient crossopterygian fishes, an order represented by the modern Polypterus and Calamoicthys, the Dipnoi being regarded as a parallel rather than an ancestral line. The Reptilia, as represented by their most primitive order with solid-roofed skulls (Cotylosauria, Cope, or Pareiasauria, Seeley), are believed to have sprung from that type of stegocephalian Amphibia which possessed rachitomous vertebræ, or with centra and intercentra. This division between reptiles and amphibians must have occurred as far back as the base of the Permian, or even in the Upper Carboniferous, because in the Middle Permian we find several orders of highly specialized reptiles, namely, the Cotylosauria, Cope, Proganosauria, Baur, Dicynodontia, Owen, and Theriodontia, Owen, highly specialized in the so-called Gom-

[1] A paper presented in part before the British Association for the Advancement of Science at Toronto, and in full before the New York Academy of Sciences. Jan. 10, 1898.

phodontia and Cynodontia. Allied to the Proganosauria, moreover, are such widely diverse types as Palæohatteria, Protorosaurus, and Kadaliosaurus.

The origin of the Mammalia is enshrouded in still more doubt. Without the aid of paleontology, Huxley, in 1880, related his Hypotheria, or oldest types of mammals, to the ancient Amphibia.

In the writer's full notes upon Professor Huxley's lectures delivered in his course of 1879–80 occurs the following sentence: "When we find a form that bridges over this gap (that is, between lower vertebrates and mammals) it will in all probability have *a double condyle caused by a reduction of the basioccipital and increase of the exoccipital parts*. The quadrate will have begun to diminish and the squamosal to enlarge, coming into relation with the angular and surangular. That this promammal will be discovered when the immense number of reptilian remains from the older rocks are studied I myself have little doubt." This the writer regards as a more successful forecast than that published by Huxley a year later. At this time he was evidently thinking over his now famous paper of Dec. 14, 1880,[1] in which occurs the following paragraph: "Our existing classification has no place for this submammalian stage of evolution (already indicated by Haeckel under the name of *Promammale*). It would be separated from the Sauropsida by its two condyles, and by the retention of the left as the principal aortic arch; while it would probably be no less differentiate from the Amphibia by the presence of the amnion and the absence of branchiæ in any period of life. I propose to term the representatives of this stage Hypotheria; and I do not doubt that when we have a fuller knowledge of the terrestrial vertebrata of the later Palæozoic epochs, forms belonging to this stage will be found among them. . . . Thus I regard the amphibian type as a representative of the next lower stage of vertebrate evolution. From the Hypotheria, as schematically shown on page 659, in which the mandible articulates with the quadrate, were derived the Prototheria, in which the large free malleus takes the place of the quadrate; from this type sprang the Metatheria, and from these, in turn, the Eutheria."

It is clearly implied by Huxley that the promammal had the paired occipital condyle of the ancient Amphibia, — an assumption of great morphological importance, and differing from that expressed in his earlier lecture quoted above. He also, in his preconception of the homology of the quadrate with the malleus, lightly passes over the difficulty of freeing the quadrate from the squamosal, to which it is closely joined in all the Amphibia. In brief, this brilliant paper lacks the author's usual unsparing logic.

[1] On the Application of the Laws of Evolution to the Arrangement of the Vertebrata, and More Particularly of the Mammalia. *Proc. Zool. Soc. of London*, Dec. 4, 1880, p. 659.

This amphibian hypothesis has recently been supported by Hubrecht (1896), who upon embryological grounds specifically connects the mammals with the stegocephalian Amphibia.

He concludes his very interesting and suggestive lecture, "The Descent of the Primates," by the passage (p. 31): "In fact, there is really not one potent reason which would prevent us from deriving arrangements, as we find them in the placental mammals, directly from viviparous amphibian ancestors." Again (p. 37): "My own choice is fixed upon the latter hypothesis, because in the Amphibia, from which I suppose the earliest placental mammals to have been derived, we find arrangements that appear to explain the origin of the amnion in the way here advocated."

There are numerous structures in the soft anatomy, not only of the monotremes, but of the placentals, which recall the amphibian type. Beddard has demonstrated the existence of an anterior abdominal vein in the monotremes. Howes [1] has compared the amphibian epiglottis with that of the mammals. Hubrecht [2] directs our attention to Klaatsch's [3] comparison of the close relations existing between the intestinal arteries of mammals and the most primitive arrangements of these vessels among amphibians. Elsewhere Hubrecht (*op. cit.*) declares that the mammals must be connected with very primitive forms that have already diverged from the common stem of the Chordata below the point of divergence of the amphibians now living, or, as we should add, from the stegocephalian type. Maurer [4] concludes that in the epidermal sense organs and hairs the mammals diverge considerably from the Sauropsida.

Cope, on the other hand, in 1884, derived the mammals from carnivorous reptiles of the group Theromorpha and order Pelycosauria.

Professor Cope, upon discovering the foot of the pelycosaurs with its supposed posterior spur, compared it with that of the monotremes, and hastened to the conclusion that these animals stood very near the ancestors of the mammals. He was long on record as deriving the Reptilia from the Batrachia with *embolomerous* (rather than rachitomous) vertebræ, and from the pelycosaurian Reptilia, the Mammalia. In his *Primary Factors of Organic Evolution*, 1896, he writes: "I have traced the origin of the mammal to theromorous reptiles of the Permian." In this latest expression of his opinion upon the subject, however, he divided the Theromora into Theriodontia, Pelycosauria, and Anomodontia, and upon the opposite page

[1] G. Howes, *Proc. Zool. Soc. of London*, 1887, p. 50.

[2] *Op. cit.*, p. 38.

[3] H. Klaatsch, Zur Morphologie der Mesenterialbildungen am Darmcanal der Wirbelthiere. *Morph. Jahrb.*, Bd. xviii, Sec. 643.

[4] F. Maurer, *Morph. Jahrb.*, Bd. xviii.

gave a phylogeny of the Mammalia, which showed that his latest views coincided with those here expressed, and that he recognized the force of Baur's criticisms cited below.

Baur in 1886 dissented from Cope's specific conclusion, but committed himself to the theory of indirect reptilian origin of the mammals, by substituting the term Sauro-mammalia for Huxley's Hypotheria, and placing the Theromorpha as parallel, rather than ancestral, to the Mammalia.

Professor Baur's paper of 1886, "Ueber die Kanäle im Humerus der Amnioten," demonstrated that the known Theromorpha are much too specialized to be regarded as ancestors of the mammals, as Professor Cope supposed. To the hypothetical group which gave origin to both Theromorpha and Mammalia Baur gave the name Sauro-mammalia, expressing a similar view in his essay of 1887, "Ueber die Abstammung der Amnioten Wirbelthiere," *Gesell. f. Morph. u. Physiologie*, München, 1887. In his recent paper (1897), showing that the pelycosaurs are highly specialized reptiles, Baur, however, gave his strong adherence to the theriodont ancestry as follows: "We are fully convinced that among these South African forms, one of which (Tritylodon) was for a long time considered a mammal, we have those reptiles which might be considered as ancestral to the mammals, or at least closely related to their ancestors. Further finds and careful critical observations have to decide this." [1]

The writer, in his university lectures of 1896, advocated the same view, having been strongly impressed during the previous year with Professor Seeley's descriptions of Cynognathus and the Gomphodontia.

Osborn,[2] in 1888, selected the Upper Triassic mammals Dromatherium and Microconodon as types of the mammalian order Protodonta, with teeth transitional between those of reptiles and mammals. Subsequently, in 1893,[3] he accepted Baur's view, deriving both the Promammalia and Theromorpha from Permian Sauro-mammalia.

In fact, Cope long diverted our attention from these South African theromorphs, which as originally perceived by Owen in 1876 are full of mammalian analogies, to the pelycosaurs

[1] On the Morphology of the Skull of the Pelycosauria, and the Origin of the Mammals. By G. Baur and E. C. Case. Zoological Club, University of Chicago, February 10; also *Science*, April 9, 1897, pp. 592–594.

[2] On the Structure and Classification of the Mesozoic Mammalia. *Journ. Acad. Nat. Sci.*, p. 251, Philadelphia, 1888.

[3] Rise of the Mammalia in North America. *Proc. Am. Assoc. Adv. Sci.*, p. 188, 1893.

which prove to be unrelated to the theromorphs and still less to the mammals.

The most important series of explorations in the Karoo Beds of South Africa, directed by Professor Seeley, thus turn our thoughts upon the origin of the mammals into the old channel considered by Owen, in spite of his indefinite views of evolution. The animals first described by him as Cynodontia and later as Theriodontia in 1876, both terms being given in full recognition of the resemblances which these animals presented to the Mammalia in their teeth, are, thanks to these explorations, very much more fully known. Seeley's successive memoirs

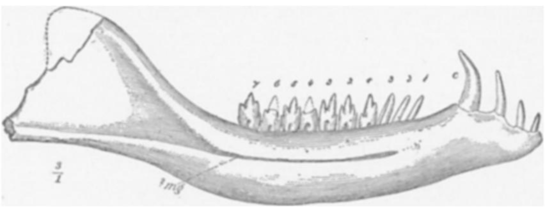

FIG. 1. — Jaw of *Dromatherium sylvestre*, a protodont from the Upper Triassic of North Carolina.

detail many of their numerous points of likeness to the recent and extinct Mammalia. These memoirs may therefore be reviewed in connection with previous speculations as to the ancestry of the mammals. We may critically consider the question of resemblances, in order to determine how far we are justified in supporting the hypothesis that the mammals sprang from the theriodont reptiles.

Seeley (1896, pp. 183, 184) has recently referred the species *Labyrinthodon rütimeyeri* of Wiedersheim to a new genus, Aristodesmus. After pointing out the numerous resemblances of this form to the monotremes, he closes as follows :

In conclusion, the author argues that the points of structure are so few in which monotreme mammals make a closer approximation to the higher mammals than is seen in this fossil and other Anomodontia that the monotreme resemblances to fossil reptiles become increased in importance. He believes that a group Theropsida might be made to include Monotremata and Anomodontia, the principal differences (other than those of the skull) being that monotremes preserve the marsupial bones, the atlas vertebra, and certain cranial sutures. Ornithorhynchus shows prefrontal and postfrontal bones, and has the malar arch formed as in anomodonts.

Aristodesmus, which suggests this link, is at present placed in the Procolophonia, a group separated from its recent association with Pareiasaurus, and restored to its original independence because it has two occipital condyles, with the occipital plate vertical and without lateral vacuities, and has the shoulder girdle distinct from Pareiasauria in the separate precoracoid extending in advance of the scapula.

A similar view is that of Mivart, who removes the monotremes so far from the marsupials and placentals as to conclude that they arose from sauropsidan ancestors, while the higher mammals, marsupials and placentals sprang independently from Amphibia-like stem forms.[1]

I. CHARACTERS OF THE PROMAMMAL.

It is obvious that to establish a point of connection we should first take characters furnished by the most ancient members of the class of mammals and picture the mammalian prototype or promammal.

As regards the teeth, I made such an attempt in 1893 (*Rise of the Mammalia*) in the following terms:

> The Permian Sauro-mammalia (Baur) with a multiple succession of simple conical teeth divided into: (1) Theromorpha, which lost the succession and in some lines acquired a heterodont dentition and triconid single-fanged molars; (2) Promammalia. The hypothetical Lower Triassic Promammalia retained a double succession of the teeth; they became heterodont, with incipient triconid double-fanged molars, the dental formula approximating 4, 1, 4–5, 8. They gave rise to three groups: (*a*) The Prototheria, which passed rapidly through the tritubercular into the multitubercular molars in the line of multituberculates, and more slowly into trituberculy, and its later stages in the line of monotremes. (*b*) They gave off the Metatheria, or marsupials, and finally (*c*) the Eutheria, or placentals.

In the same address I took very positively the position that the simple reptilian cone is the ancestor of the multitubercular as well as of the tritubercular dental types, and that the multituberculate teeth observed in the Triassic were not primitive, but had precociously passed through a tritubercular stage. I derived the characters of the promammal from a study of all the known Jurassic Mammalia. The inference as to the multiple succession of the teeth I subsequently based upon the recent embryological demonstration that all living mammals are diphyodont and sprang from polyphyodont ancestors (a principle that

[1] *Proc. Roy. Soc.*, vol. xliii, p. 372.

has recently been thrown in doubt by Woodward). The hypothesis as to the derivation of the multitubercular from the tritubercular teeth was based upon the fact that certain rodents, although unquestionably of trituberculate origin, present typical multituberculate teeth. Summing up as follows: The *Lower Triassic ancestors of monotremes, marsupials, and placentals possessed teeth differentiating into different kinds (incipiently heterodont), molars with three cones (triconodont) and dividing fangs (Proto-*

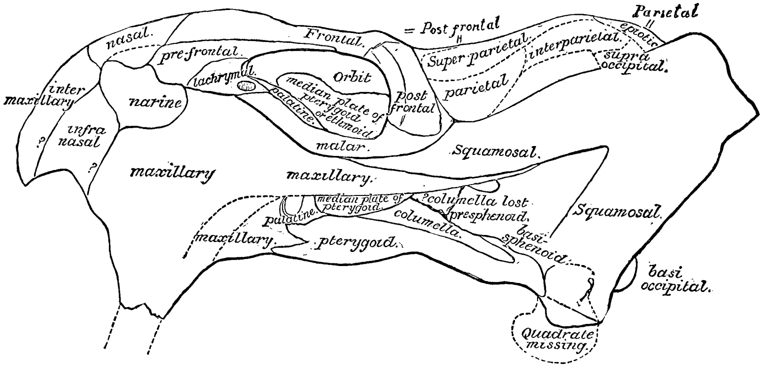

FIG. 2. — Lateral view of the skull of Dicynodon, showing Seeley's interpretation of the cranial elements. (After Seeley.)

donta), giving rise both to the multituberculate and trituberculate types, with the dental formula: incisors, 4; canines, 1; premolars, 4 or 5; molars, 8.

These assumptions are in a measure confirmed by Professor Seeley's discoveries, but the Theromora in the large sense reassume a position *ancestral* to rather than *parallel* with the mammals. Before bringing out all the grounds for this statement let us review the osteological and dental promammal characters side by side with theriodont characters.

II. History of Discovery.

Professor Owen defined the Theriodontia in 1876 as follows: "Dentition of a carnivorous type; incisors defined by position, and divided from molars by a large laniariform canine on each side of both upper and lower jaws, the lower canine crossing in front of the upper; no

ectopterygoids; humerus with an entepicondylar foramen; digital formula of fore foot, 2, 3, 3, 3, 3 phalanges."

No definition could be clearer, and upon the following page Owen suggests the hypothesis that these forms may have given rise to the mammals "by secondary law, the mode of operation of which we have still to learn."[1]

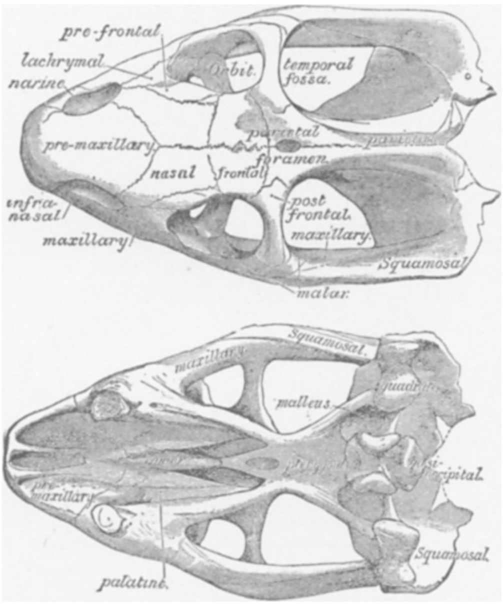

FIG. 3. — Palatal and superior views of the skull of Dicynodon, showing the elements as interpreted by Professor Seeley. Note especially the exposure of the vomer, the large extension of the squamosal, the pre- and postfrontals, the single squamoso-maxillary bar.

This definition was subsequently enlarged by Owen himself, and has been extended by Seeley. So that now this order includes forms having great diversity in their dentition, but apparently related in their osteological characters.

Thus, says Seeley (1895, 1, p. 997), the Theriodontia as originally defined included: first, the group of animals with skulls formed on the type of Lycosaurus[2] with simple pointed teeth; second, the group with skulls formed on

[1] *Quar. Journ. Geol. Soc.*, pp. 95–101, May, 1876.

[2] With this group of theriodonts Case, in a recent paper (*American Naturalist*, February, 1898, p. 73), also associates the Lycosauria; Lycosaurus being a type which furnishes a transition from the supposed fusion of the upper and lower temporal arches into the single zygomatic arch of the Mammalia, as shown in the following synopsis:

Cynodontia: Quadrate covered by supporting bones. Teeth showing small lateral tubercles. Arches more closely approximated than in Procolophonia.

Lycosauria: Quadrate small, covered by supporting bones. Skull depressed. Teeth with well-developed tubercles. Arches united.

Gomphodontia: Quadrate very small and inclosed in squamosal. Teeth tuberculate. Palate mammalian. Arches united.

the type of Thrinaxodon, which lacked the incisor teeth. One of the principal features in common is the structure of the palate, resembling that of the Mammalia in the opening of the palato-nares between the molars.

Seeley distinguishes the theriodonts from the dicynodonts by the following characters: The postorbital arch is similar, but in the theriodonts the malar bone has a greater backward extension, and in the dicynodonts the squamosal has a greater downward development, the latter difference being due to *the degeneration of the quadrate in the theriodonts.* Dicynodon, moreover, has a tripartite condyle, as in the Chelonia (composed equally of basi- and exoccipitals); while the theriodonts have paired condyles, as in the Mammalia (1895, 5, p. 129), with a depressed basioccipital portion. Both types show mammalian analogies in the palate, as well as a fixed and reduced quadrate.

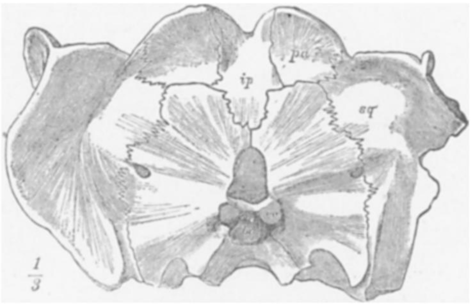

FIG. 4. — Posterior view of the occiput of *Ptychosiagum declive.* A dicynodont, showing the tripartite structure of the occipital condyle, the large interparietal, the extension of the squamosal upon the occiput. The bones lettered *pa* correspond in position with the epiotics in the labyrinthodont amphibia. (After Lydekker.)

In the palate of Dicynodon the palatine bones are separated by the vomers in the median line. The occiput is broad and flat, bounded by the parietals and interparietals above, there being a deep notch in the median line. The bones doubtfully described by Owen as paroccipitals ("opisthotics" of Huxley) are fused with the exoccipitals, as observed by Huxley in Ptychognathus and by Seeley in other forms. Laterally, the occiput is formed by the *squamosals*, elements which are very extensively developed in Dicynodon, largely covering the quadrate and descending to form *nearly half of the glenoid facet for the lower jaw*, a very important character. In this respect this genus is more mammalian than the theriodonts, in which the squamosal does not form part of the glenoid facet.

In the palate, however, the theriodonts are more mammalian, since the palatine bones meet in the median line defining the posterior nares. In both types the orbits are closed posteriorly by the postorbitals and postfrontals. The zygomatic arch in both has a large malar as well as a large squamosal.

The shoulder girdle in both presents a metacoracoid and epicoracoid, the latter perforated by a foramen, as well as a clavicle and interclavicle, thus strongly resembling the monotreme type. Dicynodon, like Gomphognathus among the theriodonts, has a decidedly promammalian type of humerus, with a prominent deltopectoral crest, an entepicondylar foramen, and prominent ent- and ectepicondyles. The pectoral arch exhibits a narrow scapula and large epi- and metacoracoids entering also into the glenoid fossa. The pelvis shows an ilium expanded above, a ventrally united ischium, and pubis with a rudimentary obturator foramen, all three bones entering equally into the acetabulum.

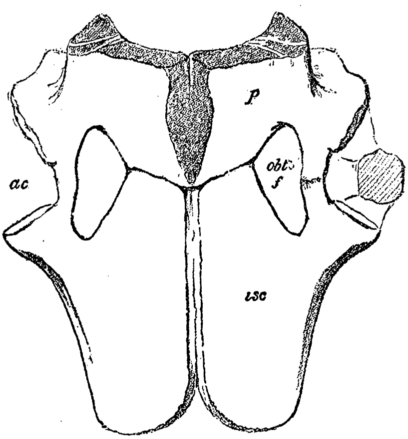

FIG. 5.— Ventral aspect of the pelvis of Cynognathus, showing the relations of the pubis, the ischium, obturator foramen. (About $\frac{1}{3}$ natural size. After Seeley.)

It is clear that the dicynodonts and theriodonts hail from a common stock, the superorder Thermora of Cope, the former showing the greater specialization and aberrancy. To this superorder the term Anomodontia is given by most English authors, but it is inapplicable, because Owen invariably defined the Anomodontia in such a manner as to embrace only the dicynodonts. The first comprehensive term was that given by Cope.

III. ORDER THERIODONTIA, OWEN.

It is a most striking fact that the theriodonts proper appear to include two suborders, which, so far as we know, are as

closely united in skeletal characters as they are dissimilar in dental characters. These are:

1. Suborder *Cynodontia:* Carnivorous animals, with cutting triconodont molars.

2. Suborder *Gomphodontia:* Herbivorous animals, with triturating, low-crowned, tritubercular and multitubercular teeth.

The teeth of these animals are even more widely differentiated than those of the Mesonychidæ and Arctocyonidæ among the Creodonta. Compared with living types, they are as wide apart as those of Thylacinus and Mus. Upon the "tritubercular theory" the dentition of the cynodonts is the most primitive. Upon the "multitubercular theory" it would be considered the most specialized.

The skeleton of the Cynodontia is by far the best known.

1. *The Cynodontia.*

The most perfectly known type is Cynognathus. The skull of Cynognathus is over a foot (15¾ inches) long. This animal was a large and powerful carnivore, the tooth structure

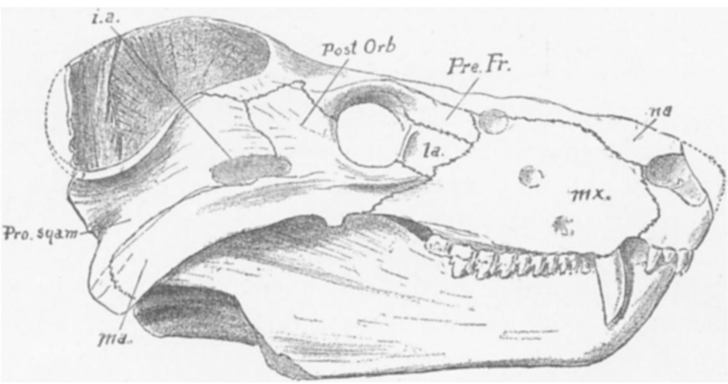

Fig. 6. — Lateral view of skull of *Cynognathus crateronotus*, showing the dentary element in the mandible; the incipient angle; the compound nature of the zygomatic arch, with an open infratemporal fossa, *ia*. (⅖ natural size. After Seeley.)

superficially resembling that of Thylacinus or Dissacus. The skull widens posteriorly, but in lateral view it is strikingly mammalian and cynoid (1895, 5, p. 61). The anterior nares are divided, terminal and lateral, the snout as seen from above

being bulbous, as in Tritylodon, covered by long nasals with a short free portion. Large lachrymals, and, conforming with the carnivorous habit and strong temporal muscles, there is a high sagittal crest, deep temporal fossæ and a strong, deep zygomatic arch, powerful chin and coronoid process (formed from the dentary). The serrated teeth agree in number with Osborn's promammalian formula, consisting of four incisors, powerful canines, five pointed and basal cusped premolars, and four triconid molars. As in the Protodonta, the molar fangs are slightly grooved, indicating a division into two roots.

There are also incipient traces of a cingulum (1895, 5, Fig. 2) and some evidence that there was a succession of the teeth

FIG. 7. — Lateral view of the teeth of *Cynognathus crateronotus*, showing the five simple premolars and triconodont molars with grooved fangs. (½ natural size. After Seeley.)

(1895, 5, p. 62). All these are promammalian characters. A close approximation to this type is in the marsupial Triconodon of the Upper Jurassic. Professor Seeley has pointed out (1895, 5, p. 90), also, that there exists a still closer resemblance between this type and Microconodon.

A perforation behind the orbits, which Cope and Baur, and very recently Case,[1] have considered as possibly representing the infratemporal fossa, is regarded by Seeley as a vacuity. Upon page 74 (1895, 5) Seeley also compares this vacuity with the infratemporal fossa. According to this interpretation, the mammalian zygoma was originally a compound structure, composed of the squamosal + prosquamosal above and the quadratojugal below. A palate, formed apparently by hori-

[1] *American Naturalist*, February, 1898, p. 73. This paper contains a valuable critique of the same subject from the standpoint of the temporal arches.

zontal palatine and maxillary plates, and two (exoccipital) condyles complete the mammalian facies.

The origin of the paired occipital condyles of the Mammalia is a matter of great importance. We observe a tripartite condyle in Dicynodon and in the Chelonia, into which the basi- and exoccipitals enter about equally; certain types of Lacertilia, such as Uroplates and Gecko (*fide* Cope), also evidently acquired their bipartite condyles secondarily by the recession of the median basioccipital element. It would appear, therefore, that the theriodonts, in which this median basioccipital element is still quite prominent, also acquired the paired exoccipital condyle in the same manner, *i.e.*, secondarily, or from the tripartite type, such as that seen in Dicynodon. We would thus have the explanation of the development of this paired structure from a reptilian tripartite condyle, as in Huxley's original conjecture, rather than directly from an amphibian paired condyle, for in the Amphibia the paired condition of the condyles arises in an extremely early period, rather than by a secondary recession of the basioccipital element.

FIG. 8.—External and anterior views of the left shoulder girdle, supposed to belong to Cynognathus, showing the scapula, parts of coracoid, precoracoid, and precoracoid foramen. ($\frac{1}{3}$ natural size. After Seeley.)

Of the transitional characters of Cynognathus, the reduced and overlapped quadrate is what we should expect to find in a promammal upon the Albrecht-Cope-Baur theory that the quadrate in the mammalia is fused with the squamosal. Among the reptilian characters are the separate prefrontal and postfrontal elements (the postorbitals being united with the malars), as well as the constitution of the lower jaw out of distinct elements (angular, articular, dentary, splenial), which by reduction and

fusion with adjacent elements might, however, pass into a mammalian prototype.

Some of the peculiar adaptive features of this type are the very elevated position of the squamosals (as in certain plesiosaurs); the paroccipitals or opisthotics exhibit large posterior vacuities, as in Dicynodon, and are united with exoccipitals; basioccipitals narrow; the epiotics are said to be separate (1895, 5, p. 77); the alisphenoids and orbitosphenoids are defined; laterally we observe descending plates of the pterygoids or "transverse-palatine" bones.

The angular region of the jaw of Cynognathus is unfortunately wanting, but it is improbable that the placental type of angle was present. Seeley points out (1895, 5, p. 90) that the rudimentary mammalian angle may consist of the posterior border of the dentary, and concurs with Osborn [1] *that the angle arose anteriorly on the lower border of the jaw* (as perhaps in Microconodon, Amphitherium, and Peramus) *and was subsequently shifted backwards.*

Remains of the shoulder girdle show that a coracoid (metacoracoid) and epicoracoid with foramen were present (as in Dicynodon), and more striking still as a point of resemblance to the monotremes is the spine and acromion of the scapula, consisting of "the anterior edge of the scapula developed upward" (1895, 5, p. 92).

Of the vertebræ preserved (1895, p. 97) there are six cervicals, eighteen dorsals, five lumbars; the first of these has the spine and odontoid process characteristic of the mammalian axis, the atlas being probably lost. The formula is estimated as: C.–6, D.–18, L.–5, S.–4. The writer has estimated the dorsolumbar formula of the primitive mammal at D. = 15, L. = 5, or D.L. = 20. The cervicals exhibit large intercentra (structures seen in a vestigial form in embryonic Insectivora and other mammals), to which, as well as to the centra, the heads of ribs are partly attached, certainly in the case of two vertebræ (*op. cit.*, p. 99), while the rib tubercles unite with the pleurapophyses of the vertebra posterior in true mammalian fashion. In the *dorsal* region (*op. cit.*, p. 104) no intercentra are described;

[1] See *Mesozoic Mammalia*, p. 223.

the heads of the ribs are intercentral or articulate between the centra and the tubercles to the succeeding vertebræ (as in mammals). Certain structures in the dorsal (D.–12) vertebræ resemble a zygophen-zygantrum articulation, compensating perhaps for the imperfectly developed zygapophyses. In the poste-

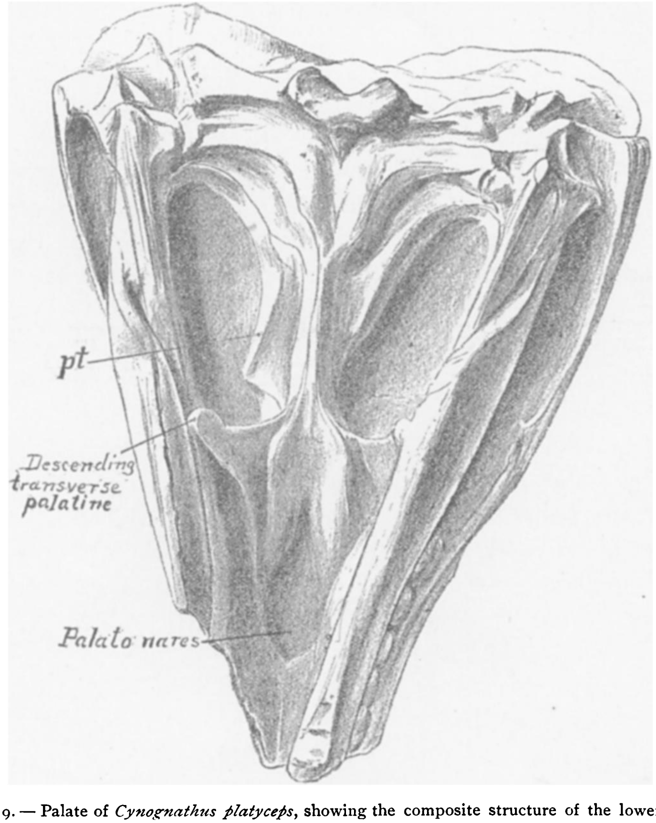

FIG. 9. — Palate of *Cynognathus platyceps*, showing the composite structure of the lower jaw, the descending transverse plates of the palatines, occipital condyle with a large basioccipital element. (⅔ natural size. After Seeley.)

rior dorsals the ribs are suturally anchylosed to the vertebræ and extend outwards into overlapping plates. Only two of the supposed sacrals are anchylosed.

The pelvis is remarkably mammalian in the structure of its ventrally united ischium and pubis, with obturator foramen (rudimentary in Dicynodon), the three bones forming the acetabulum. But it differs from the early mammalian type in the widely

expanded supra-iliac border. There is some evidence of the existence of marsupial bones, as in the monotremes and marsupials (*op. cit.*, p. 117). The femur, so far as preserved, is less mammalian in type; the trochanter minor is very prominent and extends far down the shaft.

All the above characters are observed in the single skeleton of *C. crateronotus*. In skulls of *C. berryi* are found two condyles formed from exoccipitals only (*op. cit.*, p. 129), separate pre- and postfrontals, greater coalescence of the jaw elements, an inferior dental formula estimated at:

I, 3.–C, 1.–P, 4.–Ṁ, 5.

Another species, *C. platyceps*, an animal about the size of a wolf, lacks the supposed infratemporal opening (Fig. 10) above the malar arch. The quadrate is hardly distinguishable from the squamosal. The lower jaw exhibits evidence of a splenial (*op. cit.*, p. 140) in process of degeneration. A third species,

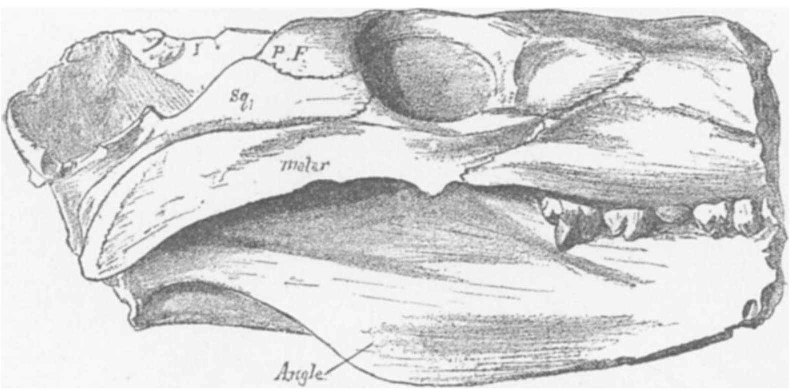

FIG. 10. — Lateral view of skull of *Cynognathus platyceps*, showing the union of the prosquamosal and malar elements, closing in the infratemporal fossa. Angle developed as in Microconodon. (After Seeley.)

probably generically distinct, is *C. leptorhinus*, with a median nasofrontal pit upon top of the face and two specialized canines.

A carpus doubtfully referred to Cynognathus (1895, 5, p. 145) exhibits elements which Seeley interprets as a united scapholunar, cuneiform, pisiform, and portions of the centrale.

2. *The Gomphodontia.*

All the remains of this group have been found in the upper Permian Beds of Ailwell North and Lady Frere, contemporary with the specialized theriodonts. The geological position of Tritylodon is not certainly known, but the other gomphodont genera, Gomphognathus, Microgomphodon, Trirachodon, and Diademodon, are certainly located in these upper Karoo Beds, and are below the Stormberg Beds, which are considered Triassic. Seeley (1895, 4) confidently places these animals in the order Theriodontia (contrasting them with the carnivorous Cynodontia) as typical herbivorous forms with molar teeth flattened and expanded transversely and more or less tuberculate crowns. The cranial and skeletal characters, so far as they are

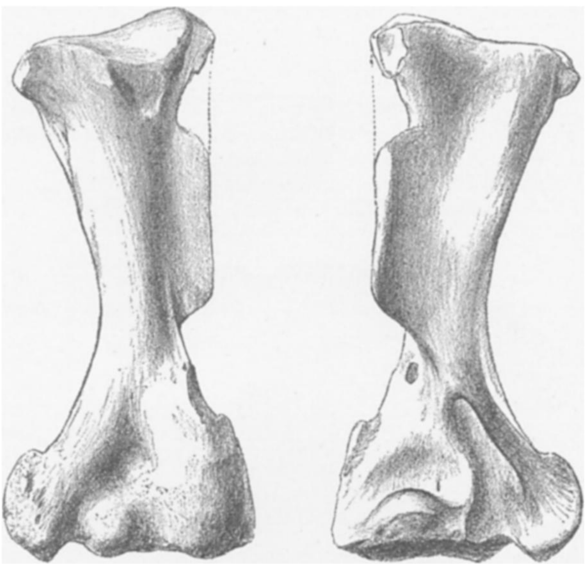

FIG. 11. — Anterior and posterior views of a right humerus referred to Gomphognathus, showing powerful deltoid crest, entepicondyle, entepicondylar foramen; separate articular facets for radius and ulna. (½ natural size. After Seeley.)

known, support Seeley's conclusion, and the wide diversity in the structure of the teeth does not alone constitute a sufficient ground for the separation of these herbivorous forms from the carnivorous Theriodontia. If Tritylodon belongs to this group,

as seems to be very probable if not absolutely demonstrated, it is certainly the most highly specialized, in the possession of strongly developed intermediate tubercles on the upper molars, which are only feebly developed in Diademodon.

The skull is partly known in the genera Gomphognathus, Microgomphodon, and Trirachodon. As in the Cynodontia, the temporal fossæ are separated by a more or less distinct sagittal crest, less prominent than in the Cynodontia because of the reduction of the temporal muscles. As in the Cynodontia, the zygomatic arch is formed by the malar and squamosal bones, and the orbit is separated from the temporal fossa by the post-orbital (postfrontal, Seeley) bone. There are two well-defined occipital condyles at the back of the base of the skull, united to each other inferiorly in a way that is closely paralleled in some mammals. The occiput is triangular and more or less concave. It lacks the large lateral foramen which distinguishes the occiput in the carnivorous Cynodontia. Externally at the sides of the occiput there is a deep notch where the squamosal bone is given off to the zygoma. The malar bone extends behind the orbit as in the mammals, and unites with the squamosal to form the larger part of the zygoma, developing a small descending process. The hard palate formed of the maxillary and palatine bones terminates in the middle of the molar region. Behind this, sharply distinguishing the palatal region from that of the mammals, there is a transverse descending arch apparently composed of the transverse bones, extending downwards so that it abuts against the rami of the mandibles, as in the Crocodilia, Rhyncocephalia, and Lacertilia. The most important resemblance to the Cynodontia is the degenerate condition of the quadrate bone, which, in the words of Seeley, "appears to be reduced to a small ossicle imbedded in the squamosal bone, but exposed in its posterior aspect behind the articular condyle of the lower jaw, into which it appears to enter."

The dentition is highly specialized. The incisor teeth are small and pointed. The canines are reduced in Microgomphodon, practically resembling the incisors. In other forms they are large, compressed, with serrated margins, as in the cyno-

donts. The homologies of this tooth in Tritylodon are uncertain. The premolar teeth are small and circular, usually tuberculate, but occasionally the first tooth is compressed laterally. The

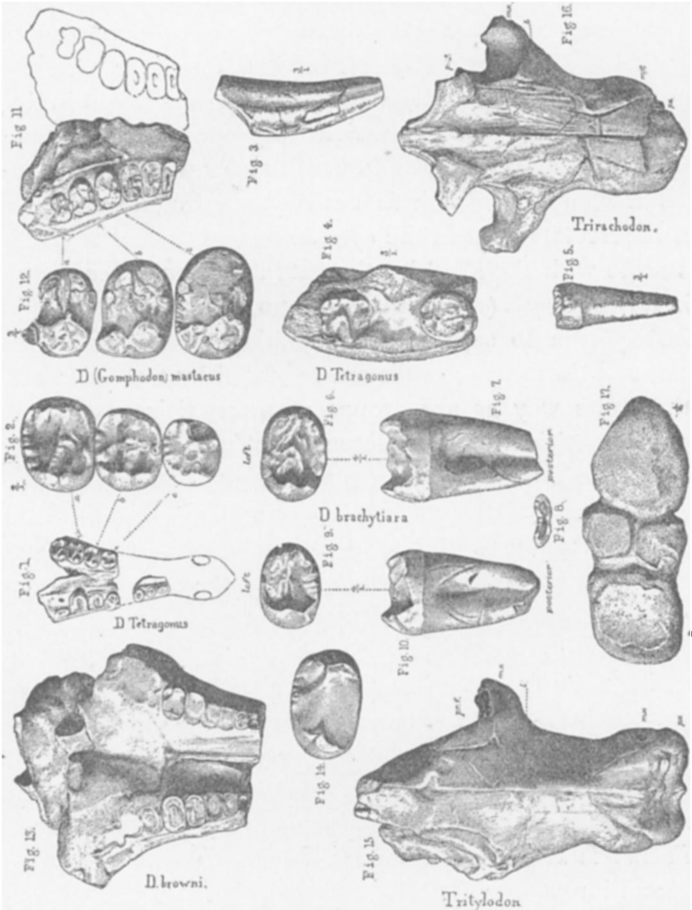

FIG. 12. — Dental and cranial structures of the Gomphodontia. *D. masticus*, analogous to a low-crowned trituberculate, like Arctocyon. *D. tetragonus*, trituberculate structure more obscure. *D. brachytiзra*, resembling the lower molars of Microlestes from the Rhætic of Germany, showing the incipient division of the fang. The skull of Tritylodon is greatly reduced. (After Seeley.)

molar teeth are usually single rooted, arranged in close-set series, which diverge sharply outwards as they extend backwards; with grinding surfaces varying in form and character, but with internal and external cusps more prominent than the

other tubercles of the crown. It is important to direct attention to this divergence of the dental series posteriorly, which shows that these animals are not typical multituberculates like Tritylodon, in which animal the dental series are parallel with each other as an adaptation to the forward and backward motion of the jaws. The lower jaws are formed, as in the theriodonts, by rami which are coalesced at the symphyses, consisting externally of dentary bones which are produced posteriorly into a high coronoid process, and exhibit also an inferior posterior angle, a character which is entirely wanting in the Eocene Multituberculata. As in the cynodonts and typical reptiles, the jaws unite with the skull by elongate articular bones.

So far as known (1895), there are no fundamental differences in the skeleton to separate the Gomphodontia from the Cynodontia, and these two groups are regarded by Seeley as related in the same way as are groups of marsupials with similarly differing dentition. The skeleton doubtfully referred to Microgomphodon shows a distal transverse expansion of the ribs into triangular extremities, as in Cynognathus, so as to form an interlocking union similar to that of the zygapophyses on the neural arch. In the same skeleton the pelvis resembles that of the Cynodontia, except in the apparent exclusion of the pubic bone from the acetabulum. For in the Cynodontia the pubis takes its normal part in forming the acetabulum. The long, lateral trochanter of the femur is less developed than in the Cynodontia. In the tarsus the astragalus and calcaneum are both large bones, but the calcaneum exhibits no tuber calcis. The scapula is constructed on the same plan as in Cynognathus. The same is true of the humerus. The interclavicle is thin, wide, and long.

Tritylodon.

The skull of *Tritylodon longævus*, described by Owen in 1884, was placed hesitatingly with the Jurassic and Eocene Multituberculata until reëxamined by Seeley in 1892 (1895, 2, p. 1025). He refers the skull to the Lady Frere level, and finds some evidence that the orbit was closed posteriorly, as among the theriodonts, Professor Owen having assumed that

the orbit was open behind. He further observes the narrowing of the skull in front of the orbits and the bulbous aspect of the snout as a more definite character relating Tritylodon to the other theriodonts. As regards the enlarged front teeth, which have hitherto been considered as incisors, he thinks it is possible, since their roots ascend into the maxillary, that they may be canines. The skull further agrees with that of the theriodonts in the terminal position of the anterior nares and in the median anterior process of the premaxillary, which forms an internarial septum, also in the position of the posterior nares opening between the hinder molar teeth. The most characteristic region of the theriodont skull is that bordering the orbit, in which, unfortunately, the type specimen of Tritylodon is imperfectly preserved, so that it is impossible to determine positively whether there was a postorbital bar composed of the postorbitals (postfrontals, Seeley) as in the Theriodontia; the fossil shows an oblique fracture at this point, and the converging plates, described by Owen as the parietal bones, are regarded by Seeley as the posterior processes of the postfrontal bones, because they are closely comparable to the similarly placed bones of the theriodonts. The prefrontal bone, on the other hand, appears distinctly as forming the antero-superior border of the orbit. "Hence," Professor Seeley concludes, "I believe that the remains of the skull go to show that Tritylodon was a reptile, and that the skull might be restored upon the theriodont plan." In the same paper Professor Seeley figures (1895, 2, p. 1028) a portion of the lower jaw.

Diademodon.

This genus was founded by Seeley on the characters of the molar teeth (1895, 3, p. 1030, Pl. LXXXIX, Fig. 11). He describes the superior molars as wider than the inferior, with the crown low, subquadrate, or transversely oval. As pointed out by the writer in *Science*, these upper teeth are of extraordinary interest, since they show *the typical tritubercular pattern.* While the crown is roughly tubercular, the four prominent cusps correspond with the protocone, paracone, metacone, and hypo-

cone, respectively, the last being much the smallest, and there are two irregular intermediate cusps which represent the conules.

These characters are fairly well seen in the species *D. tetragonus*, discovered in 1884, the type being a small skull about three inches in length. In Seeley's language (1895, 3) the general effect of this cuspidate structure is that there is a sharp cuspidate girdle surrounding the subquadrate or subovate crown, with one cusp strongly developed on the outer margin, and two strongly developed on the inner margin. He found no remains of incisor teeth in this specimen, although they may have been present. Probably associated with this type were two small canines; the reference of these teeth, however, is doubtful. There may have been three small teeth in the position of premolars and seven in the position of molars, although the fragments only indicate five.

There were two isolated molar teeth found at the same time (represented in *loc. cit.*, Pl. LXXXIX, Figs. 6–9), of very small size, which Professor Seeley doubtfully proposed as the type of the distinct species *D. brachytiara*. These teeth are extraordinarily similar to those of Microlestes of the Rhætic of Germany, hitherto regarded as a typical multituberculate related to the Plagiaulacidæ.

It is the species *D. mastacus*, however (*loc. cit.*, Pl. LXXXIX, Figs. 11, 12), which presents the significant resemblance to the tritubercular pattern in its molar teeth above mentioned. In fact, while not specifically mentioning these strong tritubercular resemblances, Seeley observes (1895, 3, p. 1037): "There is nothing with which these teeth can be compared, except the molars of some of the higher groups of mammals." The teeth, however, have but one root and belong to skulls which are undoubtedly theriodont.

In the species *D. Browni* the crown is of a still simpler tubercular pattern, with one large internal and evidences of two external cusps.

General Conclusions.

It is obvious that we must await a more complete knowledge of the skeleton of these various forms before we can confidently either classify them or establish their relations to Mammalia. The literature is in considerable confusion, and requires a more careful and exhaustive revision than I have been able to give it. It appears that the mammalian resemblances of these animals include a very large number of characters which are observed without exception in the basal Eocene or Puerco fauna of North America.

The anticipation of the triconodont and multituberculate type of dentition of the Jurassic period is remarkable. If actually phyletic, it points to an extremely early divergence of these dental types — much earlier than the period of the Protodonta.

The general resemblances with existing and basal Eocene types of mammals may be summed up as follows:

Theriodont Characters.	*Promammalian Characters.*
1. Teeth heterodont, four series; molars single rooted or with grooved fangs of triconodont and multitubercular type.	1. Same characters observed in Protodonta, Multituberculata, and Triconodonta, except that the latter have completely paired molar fangs.
2. Anterior nares terminal. Posterior nares placed far back and roofed over by palatines and maxillaries.	2. The same in basal Eocene mammals.
3. Nasals narrow anteriorly, expanding posteriorly.	3. The same in basal Eocene mammals.
4. Separate prefrontals; separate postorbitals closing orbits posteriorly.	4. No prefrontals or postorbitals. Orbits open posteriorly in all basal Eocene mammals.
5. A single infratemporal or *zygomatic* arch consisting of malars and squamosals (or consisting of fusion of upper with lower arches, Baur, Case).	5. An infratemporal or zygomatic arch only.
6. Quadrate reduced and overlapped by squamosal.	6. Quadrate probably coalesced with squamosal, occasionally separated by reversion (Albrecht).

Theriodont Characters.	*Promammalian Characters.*
7. Separate transversum as in Reptilia and a distinct prevomer in certain types.	7. Transversum and prevomer missing.
8. Paired exoccipital condyles with prominent median basioccipital element.	8. Paired condyles on exoccipitals only, with basioccipital element reduced.
9. Lower jaw composite, including dentary, articular, angular, and splenial.	9. Lower jaw composed of a single bone.
10. Cervical vertebræ with intercentra.	10. Cervicals and dorsals with embryonic intercentra in Insectivora.
11. Cervical ribs separate, suturally united with vertebræ.	11. The same in monotremes and embryos of higher mammals.
12. Anterior dorsal ribs intervertebral in position with head intercentral and tubercle neurocentral.	12. The same.
13. Scapular arch with clavicles and interclavicles; epicoracoid united by suture with the metacoracoid; prescapular spines.	13. The same in monotremes; clavicles and interclavicles wanting in higher types. Prescapular spines in monotremes.
14. Pelvic arch with ischio-pubic symphysis and rudimentary obturator foramen; acetabulum closed; pubic bones secondarily developed.	14. Pelvic arch with closed acetabulum, ischio-pubic symphysis, and large obturator foramen.
15. Carpus and tarsus imperfectly known.	15. Carpus with os-centrale; tarsus with os-tibiale.
16. Humerus with powerful delto-pectoral crest, and entepi- and ectepicondyles; entepicondylar foramen.	16. The same in all basal Eocene mammals.

Important, also, among the resemblances between the Theriodontia and Mammalia is the general body form, so far as it is known in the former, the proportions of the limbs to the back, and the apparent elevation of the body considerably above the ground. This, taken together with the peculiar specialization of the teeth into carnivorous and herbivorous types, indicates that the Theriodontia filled somewhat the same rôle in the economy of nature as is filled by the Mammalia at the present time. The most striking general difference is the very large size of several of these animals, such as Cynognathus.

We had rather anticipated from our knowledge of the earliest Stonesfield mammals that their reptilian ancestors would be very small. The large size of these Permian theriodonts, however, is not incompatible with the hypothesis that smaller and less specialized members of the group may have constituted a persistent phylum.

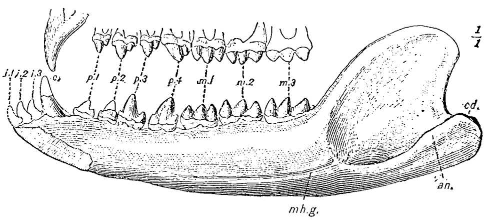

FIG. 13. — Triconodon, a typical triconodont from the Upper Jurassic, Purbeck Beds of England. (Original from specimens in the British Museum.)

The reëxamination of the jaws of the Upper Triassic Dromotherium and Microconodon fails to reveal any evidence of a composite nature, that is, so far as it is possible to determine; the jaws consist of single bones, but they are so small that this evidence is not conclusive. The position of the Protodonta, therefore, appears to be unaffected by Seeley's discoveries. The Gomphodontia of Seeley are likewise separated from the Multituberculata of Cope by the composite nature of the jaw, but it remains to be seen how far the more recent multituberculates, such as Polymastodon, which certainly have the single jaw of the mammals, may have retained other reptilian characters in the skull.

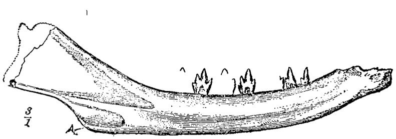

FIG. 14. — Jaw of *Microconodon tenuirostre*, a protodont from the Upper Triassic of North Carolina. *A*, supposed rudiment of angle.

We reach the general conclusion that the Theriodonts constitute a group which contains practically all the primitive characters of the Mammalia in the skeleton and teeth, and that no other reptiles or amphibians approach so near the hypothetical promammal. The explanation of the presence of amphibian characters in the soft parts of the existing Mammalia appears to be that the promammal sprang from primitive reptiles which preserved a number of still more primitive amphibian or stegocephalian characters.

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